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Reprinted from BIOLOGICAL BULLETIN, Vol. LXX, No. 2, April, 1936

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Printed in U. S. A.

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The opinion that the anterior of the three ocelli of insects really represents a pair of intimately fused ocelli is generally accepted by morphologists and is briefly expressed in several recent entomological handbooks. Thus Snodgrass (1935, p. 533) remarks that "there is evidence that the median ocellus has been formed by the union of two primitive frontal ocelli," and Imms (1934, p. 77) states more explicitly that "the median ocellus exhibits evidence of a paired origin since the root of the nerve supplying it is double, whereas the nerve-roots of the other ocelli are single. In some insects (e.g. Odonata, *Bombus*) the median ocellus exhibits a bilateral structure which is never found in the remaining ocelli." Imms' mention of the Odonata seems to refer to Hesse's observations (1901, p. 384) on *Agrion,* the median ocellus of which "has the same structure as the lateral ocelli, except that it is symmetrical. Whereas in other insects the duplicity of this eye is merely suggested by the double optic nerves, a bipartite condition is shown in *Agrion* also by the pushing in from the rostral side for some distance of a wedge of indifferent cells between the retinulæ."

Leydig seems to have been the first to detect the double innervation of the anterior ocellus. In his paper on the arthropod eye published in 1864 he says: "Concerning the optic nerves it may be said that the nerve of the median ocellus has *two roots,* each of which arises in one of the halves of the brain," and refers to the illustration (Fig. 4) of the brain of the *Formica rufa* queen in his atlas of comparative anatomy (1864*a*). This beautiful figure was reproduced by Sharp in his well-known treatise on insects in the Cambridge Natural History (1895, Fig. 65, p. 119). Among the later anatomists who have confirmed Leydig's observations on the double nerve supply of the anterior ocellus, Janet (1905) and Berlese (1909) may be mentioned.

Additional indications of the binary origin of the median ocellus are its conspicuously greater size as compared with each of the posterior ocelli in most worker ants which possess these organs and its sole persistence after the posterior ocelli have disappeared. If, however, there could be any doubt of the paired origin of the organ this has been removed by the study of its development. As early as 1887 Patten,

investigating the origin of the ocelli in *Vespa,* reached the following conclusions: "The *ocelli* of Vespa appear at the close of the larval period as *four* deep pits whose walls consist of a single layer of cells. The two anterior pits are situated close together, and soon fuse to form a single depression which develops into the anterior ocellus." . . . "The fact I desire to emphasize here, is that *the three ocelli arise from four single-layered pits, the median ocellus being formed from a coalescence of the two ventral ones.* The double nature of the median ocellus is also shown by the fact that, even in the latest stages, the root of the nerve is double, while that of the other two is single."

Apart from certain details such as the pit-like character of the ocellar primordia, Patten's observations have been confirmed by Redikorzew (1900), Zavřel (1902) and Caesar (1912). Although Redikorzew did not see the fusion of the two primordial thickenings in the honey bee, which he studied, he none the less observed the formation of the two nerves of the anterior ocellus and a very suggestive arrangement of the retinal pigment of all three ocelli. When first deposited in the retinulæ of the anterior ocellus the pigment has a remarkable bilateral distribution and that of each half is like the arrangement in each of the posterior ocelli. "From which it may be seen that each of the two halves of the median ocellus, so far as the pigment is concerned, has precisely the same structure as that of a whole lateral ocellus; in other words, it seems to be made up of two lateral ocelli."

Zavřel differs from Patten only in finding in *Vespa* that the four ocellar primordia are differentiated out of an even earlier, single "sense-plate." He gives some good illustrations of the double innervation of the anterior ocellus. Caesar has made the most thorough study to date of both the structure and development of the ocelli in ants. He describes the origin of these organs in the male of *Formica pratensis* as follows: "As in all the species of ants investigated the earliest primordia of the future ocelli make their appearance as a rule in the half-grown larvæ as four somewhat lens-shaped thickenings of the cerebral plate of the developing head-fold. Of these four primordia the two median, as shown most clearly in frontal sections, lie very close together and therefore constitute the double primordium of the future median ocellus, a proof that this ocellus has arisen phylogenetically by coalescence of two single ocelli." . . . "Concurrently with these developmental stages the lentigenous and retinogenous layers of the median ocellus fuse more and more intimately, but even in this stage a last indication of the former double origin of the whole primordium is retained in the two completely separate nerve-stands which connect it with the brain." The nearest analogue of the single anterior ocellus and its double nerve

supply among animals other than insects is the unpaired nasal sac of the cyclostome fishes with its paired olfactory nerves.

I have been led to consult the literature above cited by finding in some 15 among more than 4,000 gynandromorphs (ergatandromorphs) of a large neotropical ant, *Cephalotes atratus quadridens,* that the anterior ocellus is replaced by two smaller contiguous ocelli (Fig. 1).[1] Obviously, in these specimens the original paired primordia of the retinæ, corneagen cells and corneæ have differentiated in the adult without coalescing. Although it seemed probable that similar doubling of the anterior ocellus might occur occasionally among otherwise normal insects, I could recall no cases among the many thousands of Formicidæ

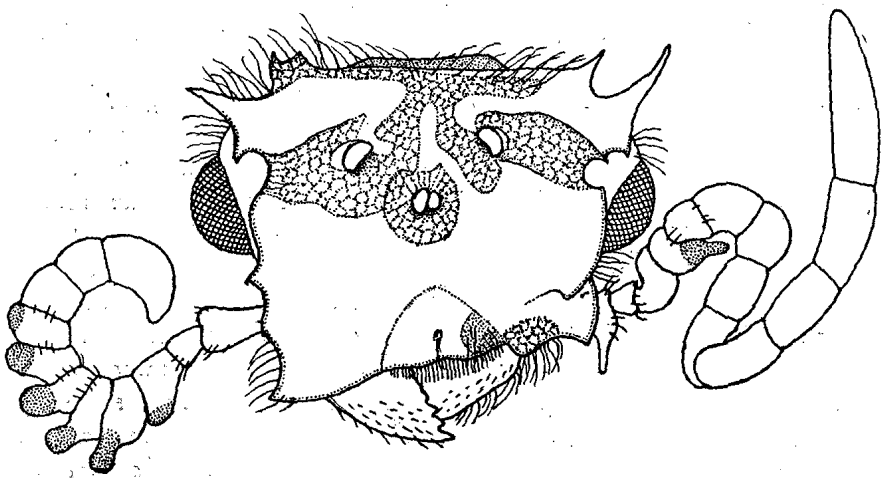

FIG. 1. Head of gynandromorph (ergatandromorph) of *Cephalotes atratus quadridens* Degeer, with binary anterior ocellus. One of several specimens. The large eyes, left mandible, thirteen-segmented left antenna, the stippled area and long hairs on the head and clypeus (except along its anterior border) and the papilla-like, stippled projections of the median joints of the right antenna are male characters.

and other aculeate Hymenoptera which I have examined during the past forty years. Moreover, my colleagues, Professor C. T. Brues, Dr. J. Bequaert, and Mr. Nathan Banks, who have a very wide acquaintance with many orders of insects, were equally certain of never having seen an example of double anterior ocellus and, like myself, could recall no reference to such an occurrence in the entomological

[1] This extraordinary number of gynandromorphs occurred in a single huge colony of *Cephalotes atratus quadridens* Degeer recently collected with great care by Dr. N. A. Weber in the island of Trinidad, B. W. I. A preliminary account of these anomalies was presented at the meeting of the British Association for the Advancement of Science in September, 1935. The final paper by Dr. Weber and myself has not yet been completed.

literature. At first sight, Comstock's general account of the ocelli in insects (1924) creates a suspicion that two ocelli may actually have been observed in some species. He says, p. 134: "When all [eyes] are present there are two compound eyes and, typically, two pairs of ocelli; but almost invariably the members of one pair of ocelli are united and form a single median ocellus. The median ocellus is wanting in many insects that possess the other two ocelli." On p. 135 he repeats this statement in a different form: "Of these [ocelli] there are typically two pairs; but usually when they are present there are only three of them, and in many cases only a single pair. When there are three ocelli, the double nature of the median ocellus is shown by the fact that the root of the nerve is double, while that of each of the other two is single." Since Comstock cites no cases of binary anterior ocellus, one suspects that the word "typically" in both these quotations is probably employed in the sense of "originally" or "phylogenetically."

After considerable search, however, I find that double anterior ocelli do occur in at least two species of myrmicine ants and I therefore believe that further investigation may reveal their presence in some other insects. The ant which exhibits this peculiarity most frequently is the huge-headed soldier, or worker maxima of the large neotropical leaf-cutting and fungus-growing *Atta cephalotes*. Linnaeus in his original description of this insect makes no mention of the ocelli, and Degeer (1773), who described it more carefully, expressly states that "the three smooth eyes are lacking." F. Smith in 1858 seems to have been the first to call attention to the large median ocellus in the worker maxima of *cephalotes* as distinguishing it from the same caste in *Atta sexdens*. According to Forel (1904) the maximæ of the former species "have three ocelli, of which the anterior is large, the two posterior small."

I have examined 300 maxima workers from series taken from some 25 colonies. Of these specimens, which comprise the typical *cephalotes* from the Guianas, Venezuela, and Trinidad, the subspecies *integrior* Forel (Brazil), the subspecies *opaca* Forel (Central America and northwestern South America) and *gorgo* subsp. nov. (Panama), more than 60 per cent have the anterior ocellus more or less distinctly divided.[2] In some of the series the percentage is even higher than 60, in others

FIG. 2. Front and ocelli of twelve specimens of the worker maxima of *Atta cephalotes*. *a*, subsp. *opaca* (British Honduras); *b* and *c*, subsp. *gorgo* subsp. nov. (Panama); *d*, *cephalotes*, typical (British Guiana); *e* and *f*, subsp. *gorgo* (Panama); *g*, *cephalotes*, typical (British Guiana); *h*, subsp. *opaca* (Ecuador); *i*, *cephalotes*, typical (Trinidad); *j*, subsp. *opaca* (Ecuador); *k*, subsp. *opaca* (Costa Rica); *l*, subsp. *opaca* (Ecuador).

[2] For a brief revision of these and other forms of *Atta* see my paper "Taxonomic Notes on the Ants of the genus Atta" (in preparation).

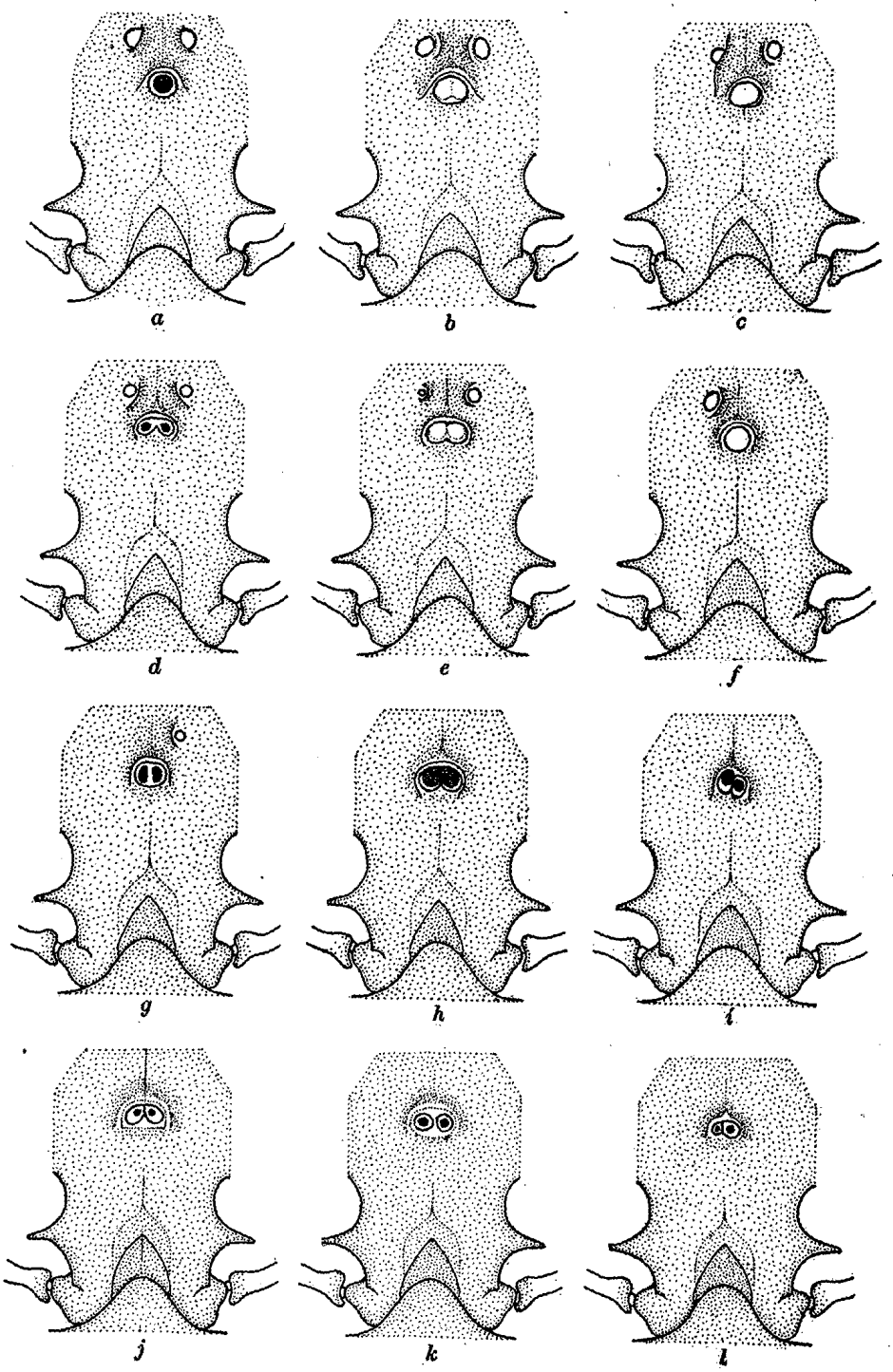

FIG. 2.

less. Thus in a series of 73 maximæ from a single flourishing and very pugnacious colony which Dr. William Beebe and I excavated at Kartabo, British Guiana, September 1, 1920, 93 per cent have a distinctly bipartite anterior ocellus. As shown in the 12 illustrations (Fig. 2), the ocelli are highly variable. Some specimens (*a–e*) possess all three

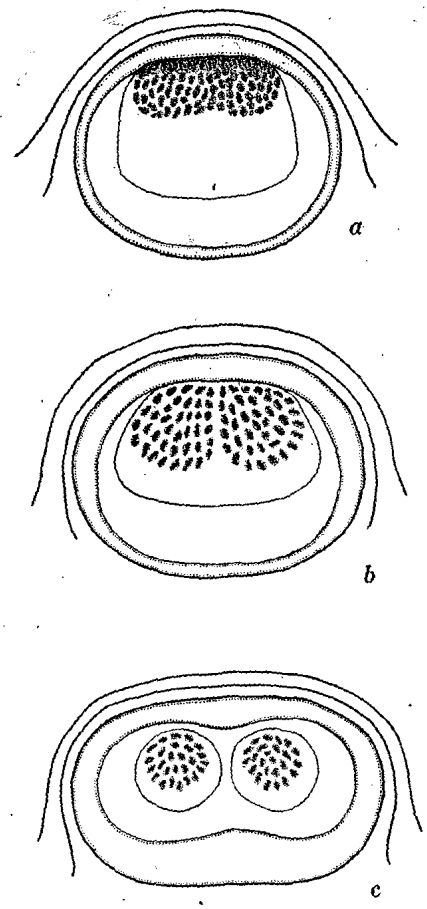

FIG. 3. Anterior ocelli of three maxima workers of *Atta cephalotes* from British Guiana seen from inside of head and showing distribution of retinal pigment under high magnification. *a*, retina with only slight and *b*, greater tendency to bipartition of retina. *c*, with two widely separated retinæ.

ocelli but one of the posterior is frequently smaller than the other (*c*, *e*) or as in *f* and *g* one of the pair has disappeared. In all cases each of posterior ocelli is decidedly smaller than the unpaired anterior ocellus. In alcoholic specimens this may have a single pigmented retina more or less clearly visible through the clear, undivided cornea (*a*), but all

stages may be observed from partially to completely divided corneas and/or retinæ (*b, d, e, g, i–l*). Occasionally one of the two members may be smaller (*l*) than the other or placed at a lower level on the front (*i*).

Portions of the front of maxima workers of *cephalotes* stained and mounted *in toto* and viewed from the inner surface of the integument under a high magnification showed little that could not be inferred from the outer surface, except the more definite arrangement of the pigment in the ommatidia. In the three preparations represented in Fig. 3 the amount of pigment in the anterior ocellus is approximately equal to that of both posterior ocelli, when these are present. In all my preparations the pigment of the anterior ocellus shows also that there are two retinæ which in some specimens are contiguous or even fused, in others separated by a very appreciable gap. The material, however, is so old and poorly preserved that other histological details cannot be discerned. The same statement applies to my sections of heads of pupal maxima workers. Hence before further investigation can be undertaken freshly fixed material will have to be obtained.

The other ant in which I have seen a double anterior ocellus is the Indomalayan *Pheidologeton diversus* Jerdon, a species which possesses a huge worker maxima like the same caste in *Atta cephalotes*. Usually only the large anterior ocellus is present, but occasional specimens also retain minute posterior ocelli. Unfortunately, my series of maximæ of this ant is rather small, but in one specimen belonging to the variety *laotina* Santschi from Saigon, the cornea of the anterior ocellus is distinctly bipartite.

The anterior ocellus in the largest workers of *Atta cephalotes* and *Pheidologeton diversus,* though large compared with either of the posterior ocelli, when they are present, is, nevertheless, a vestigial structure compared with its homologue in the cospecific male and female. When bipartite it obviously exhibits a retardation of development and persistence in a stage corresponding to the original paired hypodermal thickenings of the larva before or just after their union in the mid-dorsal line, though the corneagen and retinogen cells are differentiated beyond this stage, as shown by the secretion of the cornea and the deposition of retinal pigment. I fail, however, to detect any differentiation of rhabdomes, but this is probably due to the poor preservation of the material.

Since, as a very general rule, the two primordia of the anterior ocellus in adult insects fuse to form a single organ, we are naturally led to inquire whether in certain species there may not be a coalescence of the primordia of both pairs of ocelli. There is, indeed, some evidence

of such an occurrence. It has long been known that what authors have interpreted as the posterior pair of ocelli in Plecoptera (Ephemerida) differ from those of all other insects in having an undeveloped cornea and beneath it a cellular lens. Now Seiler (1905) has shown that the anterior ocellus of *Ephemera vulgata* is really tripartite and is supplied by *three* nerves. This investigator is therefore inclined to believe that the so-called posterior ocelli of ephemerids are not homologous with the posterior ocelli of other insects and that the anterior ocellus is really a fusion of all three typical insect ocelli. The median of the three ocellar nerves, as shown in his figure, is twice as thick as either of the others and may therefore have arisen by coalescence of the pair belonging to the anterior ocellus. At any rate, renewed comparative study of the ocelli of ephemerids might yield results of considerable morphological interest, because Seiler's work clearly suggests that the ancestors of these insects were provided with three instead of two pairs of simple, in addition to the single pair of facetted eyes.

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